Sveriges lantbruksuniversitet
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Abstract

Kattegat is an area between Denmark and Sweden that connects the Atlantic Ocean to the Baltic Sea. It has long been an important source for fishery of cod (*Gadus morhua*). In a time where the future of the Kattegat cod stock is uncertain, the relationship between the predator harbour porpoise (*Phocoena phocoena*) and the Kattegat cod remains relatively unknown. In this study, available data that can be used to assess this prey-predator relationship are compiled and evaluated, and the information gaps that need to be filled are identified and discussed. The most recent harbour porpoise abundance assessment from SCANS-III can be approximately remodelled for the Kattegat area to 23 190 (15 550-30 830) animals, eating an estimated average of 3.7 (1.9-5.5) kg of prey each day. Of this, an estimated average of 22 % (5.5-29.3) in weight is comprised of cod, a number which varies seasonally, annually and depending on age and sex of the predator. These results give a mean total annual consumption of 7 020 (593-18 150) tonnes of cod from harbour porpoises in the Kattegat.

When applying harbour porpoise predation to the stock assessment model of Kattegat cod, it is important to have accurate representations of harbour porpoise abundance and diet composition of harbour porpoise from the Kattegat region specifically. As a stock assessment model is to be used to assess potential threats in the future of the Kattegat cod stock, it is important to be able to connect these values to the variations of prey compositions available in the Kattegat, so that the harbour predation can be assessed for the future. Sufficient data is currently unavailable, and the timeframes in which the samples have been collected are too long and too old to be able to take variations over time into account. More samples from the Kattegat and would be required to make an accurate harbour porpoise predation assessment, ideally in timeframes that are comparable to the ongoing assessments of the cod stock in the Kattegat. As such data is not currently being collected, it could be possible to use available diet composition data, combined with knowledge of seasonal variations in feeding habits to make an approximation of how harbour porpoise predation varies with varying availability of cod in the Kattegat. These approximations may be used to create vague prognoses for the cod stock assessment model.

Keywords: *Atlantic cod, diet, Gadus morhua, harbour porpoise, Kattegat, Phocoena phocoena, prey*

Sammanfattning

Kattegatt är ett område mellan Danmark och Sverige som sammankopplar Atlanten med Östersjön. Det har länge varit ett viktigt område för fiske utav torsk (*Gadus morhua*). Framtiden hos torskbeståndet i Kattegatt är osäker, och trots det är fortfarande sambandet mellan predatorn vanlig tumlare (*Phocoena phocoena*) och Kattegattorsken relativt okänt. I denna studie samlas och utvärderas den tillgängliga data som kan vara till användning för att uppskatta detta samband mellan byta och predator, och de informationsluckor som finns identifieras och diskuteras. Den senaste uppskattningen av abundans för tumlare, SCANS-III, kan ungefärligt omräknas till 23 190 (15 550-30 830) tumlare i Kattegatt. Dessa äter uppskattat 3.7 (1.9-5.5) kg fisk om dagen, och uppskattat 22% (5.5-29.3%) av detta är torsk, en siffra som varierar med säsong, årsvis och beroende på predatorns ålder och kön. Med dessa resultat kan en årlig medelkonsumption beräknas till 7 020 (593-18 150) ton torsk för de tumlare som finns i Kattegatt.

När man ska applicera predation från tumlare på befintliga beståndsanalyser av torskbeståndet I Kattegatt så är det viktigt att variablerna för tumlarabundans och tumlarnas dietsammansättning är representativa specifikt för tumlare i Kattegatt. Då en beståndsanalys används för att uppskatta potentiella framtida hot mot Kattegattbeståndet av torsk så är det viktigt att man kan koppla dessa värden till variationer i sammansättning hos bytesfisk i Kattegatt, så att predationen kan uppskattas baserat på framtida antagna förändringar i bytessammansättning. I nuläget är en tillräcklig mängd data inte tillgänglig, och den tidsramar som de prover som finns har samlats in inom är för långa och för gamla för att temporala variationer ska kunna tas hänsyn till när man analyserar dem. Fler prover från Kattegatt skulle behövas för att kunna göra en precis uppskattning av tumlarpredationen, optimalt hade varit prover som tidsmässigt stammer överens med de nuvarande beståndsuppskattningar som finns för torsken i Kattegatt. Denna data samlas för nuvarande inte in, dock, så en alternativ lösning vore att kombinera nuvarande dietdata med de säsongsvisa och årvisa variationer i diet som har observerats under dietanalyser. Dessa data skulle kunna användas för att skapa en approximativ modell som visar hur tumlarnas diet varierar med förändrade bytesförutsättningar i Kattegatt. Dessa approximationer skulle sedan kunna användas för att göra en ungefärlig prognos över den framtida predationen på Kattegattorsken från tumlare.

Nyckelord: *Atlantisk torsk, byte, diet, Gadus morhua, Kattegatt, Phocoena phocoena, tumlare*

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1. Introduction

1.1 Kattegat cod stock description

Of the wild fish stocks in the North Atlantic, the Atlantic cod (*Gadus morhua*) stocks have long been some of the most economically important, to the point of gaining the nickname of *“beef of the sea”* (FAO 2017). The capture production for Atlantic cod, hereafter entitled cod, globally has seen a downward trend, and is now at only a third of 1968 levels (FAO 2017). In the Kattegat, cod has been exploited for food in for probably as long as humans have lived along the coast. Since the 1970s, the Kattegat cod stock has diminished greatly in numbers (Figure 1). In recent surveys, spawning grounds of Kattegat cod have been mapped to the south-eastern parts of the Kattegat, indicating that large concentrations of the Kattegat cod stock agglomerate there (Vitale et al. 2008).
A reduction in fishery catches can be partially attributed to the ICES Advisory Committee recommending a zero take from cod in the Kattegat in 2002 and onwards, a recommendation that comes from the stock’s severe depletion since the 1970s (Vitale et al. 2008, ICES 2017). Since these recommendations, the cod spawning stock size has recovered to some extent since the all-time low of 1366 tonnes in 2009 (Figure 1). In recent years, the Kattegat cod stock has reached late 1990s levels, but is still far from the significantly larger stock size of around 35 000 tonnes in the early 1970s (ICES 2017). In the Kattegat, cod from the local stock is mixed with juvenile cod from the North Sea stock (ICES 2014, ICES 2017).

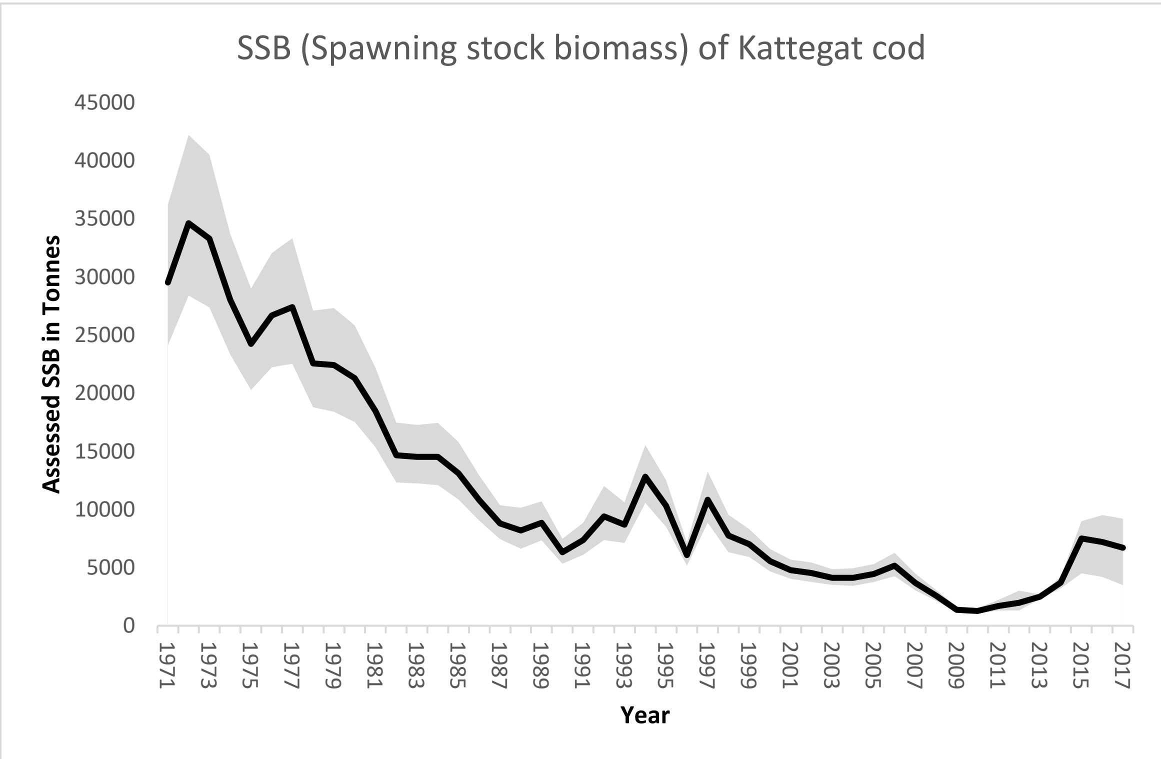

Figure 1: Assessed spawning stock biomass (SSB) of the Kattegat cod stock over the last 47 years (ICES 2012, ICES 2017).

Research has been conducted regarding the reasons for the decline in cod population size in the Baltic Sea (Eero et al. 2011). Most of these factors, including climate, predation, fishing and eutrophication, are applicable also to the Kattegat cod stock. In addition, the present large harbour seal (*Phoca vitulina*) populations in the Kattegat-Skagerrak area have raised concerns regarding the impact of the seals on fish stocks. The harbour seal population in the Kattegat has increased since the late 1970's, approaching about 9000 counted seals in the last years' censuses (Bäcklin et al. 2016), representing about 60 % of the population size (Härkönen et al. 1999). Preliminary estimates of the cod consumption by harbour seals in the Kattegat have concluded that the seals are likely to have impact on the local cod stock. The full scope of the ecological impact of the seals has not been explored yet, however (Personal correspondence, Karl Lundström SLU Aqua). However, since the harbour porpoise population in the Kattegat area has recently been estimated at much larger numbers (Hammond et al. 2017), there is likely reason to examine the potential of harbour porpoise as consumers of cod in the Kattegat.

1.2 Harbour porpoise in Kattegat

A satellite tracking study has found several key habitats for harbour porpoises within the Kattegat area, specifically around the northern edge of the Sound, by the northern Samsø Belt and near the Kalundborg Fjord (Sveegaard et al. 2011). Harbour porpoises have a high energy requirement and are considered as opportunistic predators, i.e. their choice of prey is very closely related to the prey that is most readily available in the immediate area (Lockyer, 2007). For this reason, the key habitats where harbour porpoises most commonly reside are likely in close proximity to concentrated areas of prey species.

The largest survey on harbour porpoise abundance in the Kattegat is the SCANS (*Small Cetacean Abundance in the North Sea and Adjacent Waters*) survey. This is also the one stretching furthest back in time, having started measuring as early as 1994 (Hammond et al. 1995), with subsequent surveys in 2005 and 2016 (Hammond et al. 2006, Hammond et al. 2017). This survey gave an animal density of 0.725 animals/km^2 for the Kattegat area in 1994 (Hammond et al. (1995). In 2005, the area around Kattegat had an estimated 0.28 animals/km^2 (Hammond et al. 2006). The density was once again estimated in 2012 as 0.786 animals/km^2 (Viquerat et al. 2014). The most recent survey in summer 2016 assessed the animal density in the Kattegat area to be 1.15 animals/km^2 (Hammond et al. 2017). However, even as the same survey method was used for each abundance assessment, as different methods were used to estimate animal density it is hard to make a conclusion as to how the harbour porpoise population has changed over the years.

Concerns have been raised towards the population viability of harbour porpoises, primarily in the Baltic Sea, and this can be partially attributed to bycatch, disturbance and contaminants in the waters, but also to the decline in abundance of prey species (Koschinski 2002). Thus, it is important to study the interaction between harbour porpoise predators and their prey not only for the assessment of prey species stocks, but also to further the knowledge of the necessity of management efforts for the benefit of the harbour porpoise.

In this literature study, studies on harbour porpoise abundance and prey consumption are compiled with the purpose of presenting the current knowledge about prey choice of harbour porpoises in the Kattegat and neighbouring areas. Included is also an evaluation of to what extent data required to apply harbour porpoise predation in stock assessment models of Kattegat cod can be found within available material. Gaps in information are also identified, as well as what needs to be done to complete the necessary information. The study has been limited to the relation between harbour porpoise and cod in the Kattegat only.

Similar studies have been made in the past. In Sveegard et al. (2011), studies on harbour porpoise stomach content analyses are compiled to create a diet composition and relate these to the prey availability in the Kattegat, the Baltic Sea, the Belt Seas and the Sound. This study aims to apply the conclusions of that paper and others specifically to the Kattegat cod stock, and to evaluate the results in relation to the stock assessment models that exist for cod in the Kattegat.

2. Methods

The data for this study were found with the help of studies found via SLU library databases and SLU Aqua correspondence.

2.1 Estimation of abundance

Abundance assessment data were collected from the SCANS (Small Cetaceans in the European Atlantic and North Sea) project surveys conducted in 1994, 2005 and 2016 as well as the miniSCANS survey conducted in 2012 (Hammond et al. 2017, Viquerat et al. 2014). The surveys were executed within Kattegat with the same method - ship-board double platform survey - but within different time frames and slightly different survey areas (Table 1). The survey vessels travelled along transect lines across the survey area as the number of harbour porpoises was documented, and the total distance of the transects lines in each survey is labelled Effort in Table 1.

This study is limited to the Kattegat cod stock, limiting the study area to what is commonly regarded as the Kattegat (Figure 3). As such, the abundance will be calculated for the Kattegat only. This area has its northern boundary go between the Skagen Lighthouse and the Tistlarna Lighthouse, and then to the nearest point on the Swedish west coast, and the southern boundaries delineated by straight lines drawn between Hasenöre and Gniben, and between Gilbjerdhoved and Kullens lighthouse (FAO 2017).

Table 1: Effort, timeframe and respective area for each survey. Note that the effort and surface area presented are limited to the part of the survey area that contains the Kattegat. The extent of this area varies between studies.

Survey	Year of survey	Survey area	Effort (km)	Surface area (km^2)	Reference
SCANS	1994	North Sea, Skagerrak, **Kattegat**, Belt Seas and the Baltic Sea. Also the Celtic Sea.	1 475	49 485	Hammond et al. (1995)
SCANS-II	2005	North Sea, Skagerrak, **Kattegat**, Belt Seas and the Baltic Sea. Also the Celtic Sea.	1 283	68 372	Hammond et al. (2006)
miniSCANS	2012	Southern Skagerrak, **Kattegat**, Belt Seas and the Western Baltic	826	51 511	Viquerat et al. (2014)
SCANS-III	2016	North Sea, Skagerrak, **Kattegat**, Belt Seas and the Western Baltic. Also the Celtic Sea, Bay of Biscay and the Iberian Shelf	1 243	64 158	Hammond et al. (2017)

2.2 Estimation of diet

The harbour porpoise stomach analysis studies that were chosen for this study are similar in methods. All the studies used a method where the fore stomach and lower oesophagus were rinsed with running water, and the content was then separated with several sieves, with mesh sizes of 2 mm, 1 mm and 0.5 mm, after which the separated prey remains were identified, measured and counted. The locations, timeframes and number of harbour porpoise samples were slightly different between the studies (Table 2).

The diet analysis from Börjesson et al. (2003) and Andreasen et al. (2017) studies assessed prey sizes (length and weight). These assessments were made by measuring sagittal otoliths and using otolith size-fish size regression equations presented in Härkönen (1986) or Leopold et al. (2001).

Table 2: Spatial, temporal and effort differences between the stomach content analyses in the Kattegat and neighbouring areas.

Author	Year	No. porpoises	Area
Lick 1991	1986-1990	36	Danish straits, Western Baltic
Andreasen (2009)	1985-2006	179	Kattegat, Danish straits, Western Baltic
Lick 1994; 1995 & Benke et al. 1998	1991-1994	26	Danish straits, Western Baltic
Aarefjord et al. 1995	1985 -1990	39	Kattegat
Börjesson et al. 2003	1988-1996	112	Kattegat-Skagerrak
Sveegaard et al. 2012	1987-2010	53	The Sound
Andreasen et al. 2017	1980-2011	339	Kattegat, Inner Danish Waters, Western Baltic

The results from both of the Lick surveys will henceforth be combined and referred to as Lick (1986-1994).

2.3 Estimation of daily prey consumption

Multiple estimations of daily prey consumption for harbour porpoise have been made (Table 3), mainly by measuring daily food intake of captive animals, but also by making models based on diet composition data and energy requirements.

Table 3: Daily food intake of harbour porpoise in the Baltic and North Sea

Study	Daily intake (kg/porpoise)	Methods	Sample size	Estimated daily energy consumption (MJ/day)
Andreasen et al. (2017)	1.9–5.5	Averaged from stomach content analysis, based on assumed mean, low and high energy requirements	339	10-30
Sergeant (1969)	2.0–5.4	Measurements on captive animals	8	n/a
Kastelein et al. (1997)	0.75-3.25	Measurements of recovering stranded animals in captivity	6	8-25
Yasui and Gaskin (1986)	1.78	Calculated from stomach content data	n/a	11.3
Lockyer et al. (2001)	3-4.5	Measurements on captive animals	2	16.4-35.5
Innes et al. (1987)	3.3-3.6	Calculations using energy requirement equations from terrestrial mammal predators	n/a	n/a

2.4 Application of results in a stock assessment model for Kattegat stock

To be able to include prey consumption by a predator population in stock assessment models for a prey species, several variables are required. These are (Personal correspondence, Karl Lundström SLU Aqua, Margit Eero DTU Aqua):

- Predator abundance in the distribution area of the fish stock in concern
- Diet composition of predators in the distribution area
- Daily consumption of the predator
- Size/age composition of the prey in the predator diet

These variables should also optimally be presented as a time series comparable to the time series of the stock assessment model in question.

Because of the need to limit some data to the distribution area of the fish stock in concern, in this case the Kattegat cod stock, stomach analysis studies were limited to those that overlap with Kattegat region. For this reason, the results from Sveegaard et al. (2012) and Lick (1986-1994) have been disregarded in this study. The study from Andreasen (2009) was not included since the 179 samples analysed in Andreasen (2009) are also included in the 339 samples analysed in Andreasen et al. (2017). Andreasen et al. (2017) includes samples from the Western Baltic Sea as well as the Kattegat, and a separation of data specifically from the Kattegat could not be made within this analysis.

When calculating the overall average weight percentage of prey species, the results from each study were multiplied by the amount of stomachs analysed in the study. These values were added together, and then divided by the total amount of stomachs analysed in all studies. In this way, the contribution to the total average from each study will be weighted in relation to the proportional amount of stomachs analysed in each study. Andreasen et al. (2017) divided the weight percentage results between juvenile porpoises and adult porpoises - 26% for the 228 juvenile stomachs analyzed and 36% for the 111 adult stomachs. The result presented is averaged between these two results, weighted based on the proportion of juvenile and adult stomachs.

The abundance assessment survey has also been limited to the Kattegat area, which within the SCANS-III project is represented by parts of the areas that they have labelled as subsection 1 and 2 (Figure 2). Limiting the survey area to within the ICES boundaries for the Kattegat fishing area makes a water surface area of approximately 6 780 km^2 in subsection 1 and 13 627 km^2 in subsection 2 (Area measurements made using Google Maps) (Figure 3).

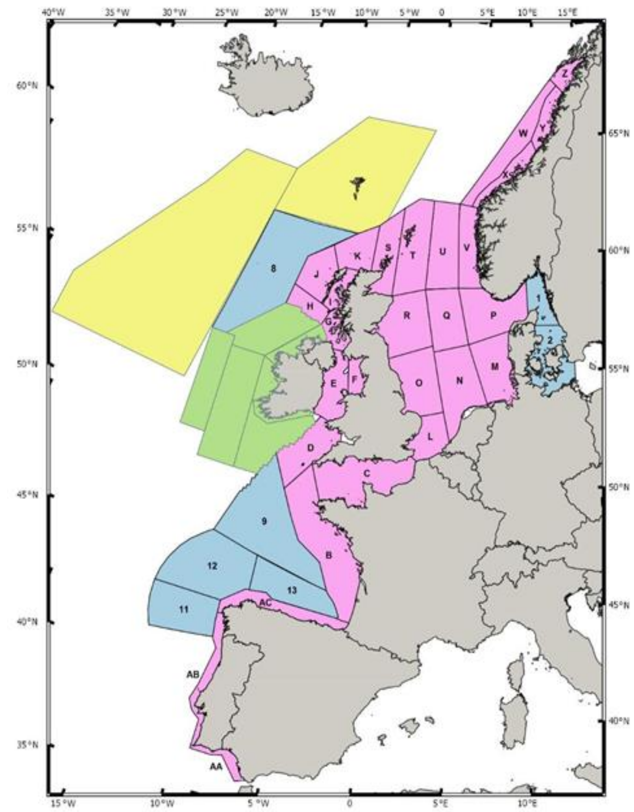

Figure 2: Survey area of the SCANS-III survey. Results for region 1 and 2 are included in this study. (Hammond et al 2017)

Figure 3: Area approximation of Kattegat, divided into subsection 1 (upper) and 2 (lower) of the SCANS-III survey (Hammond et al. 2017)

3. Results

3.1 Harbour porpoise abundance and distribution in the Kattegat

SCANS-III gave a recent abundance estimation of 73 573 (95% CI: 39 383-137 443) animals in 2016 for an area covering the area spanning between the Skagerrak and the westernmost part of the Baltic Sea (Hammond et al. 2017). When limiting the survey area to the Kattegat area, the surveys in the southern part of subsection 1 and the northernmost part of subsection 2 of the SCANS-III survey are the only ones that remain within the target area (Figure 2-3). To make an abundance assessment for the Kattegat, these values were used in conjunction with the animal densities reported in the Kattegat and neighbouring areas in SCANS-III resulting in an abundance estimate of 23 190 animals within the Kattegat in 2016 (Table 4).

Table 4: Harbour porpoise abundance in the Kattegat in 2016. Area was calculated with Google Maps using the boundaries for Kattegat in FAO (2017) and the boundaries of the SCANS-III subsections in Hammond (2017). Animal densities were gathered from SCANS-III.

	Area within Kattegat (km^2)	*Animal density (animals/km^2)*	*CV*	*Abundance assessment (animals within Kattegat)*	*CV*
Subsection 1	6 780	1.33	0.472	9 020	3 200
Subsection 2	13 627	1.04	0.304	14 170	4 140
Total	20 407	-		23 190	7 640

3.2 Diet composition of harbour porpoises in the Kattegat

The results from the three stomach analysis studies that overlapped with the Kattegat are presented in Table 5. The survey areas are presented in Figure 4.

Table 5: Proportion of total stomach contents comprised of Atlantic cod

Study	Cod proportion (W%)
Börjesson et al. (2003)	5.5
Aarefjord et al. (1995)	10.6
Andreasen et al. (2017)	29.3*
Mean	22.4

** The study made Andreasen (2017) divided weight percentage of cod by juvenile and adult porpoise samples. As such an average was calculated using the proportion of juveniles and adults presented in the study*.

Other prey species that were common in the diet studies analysed were herring (*Clupea harengus*), gobies (*Gobiidae*) and whiting (*Merlangius merlangus*). In the analysis by Börjesson et al. (2003), sprat (*Sprattus sprattus*) was also commonly seen.

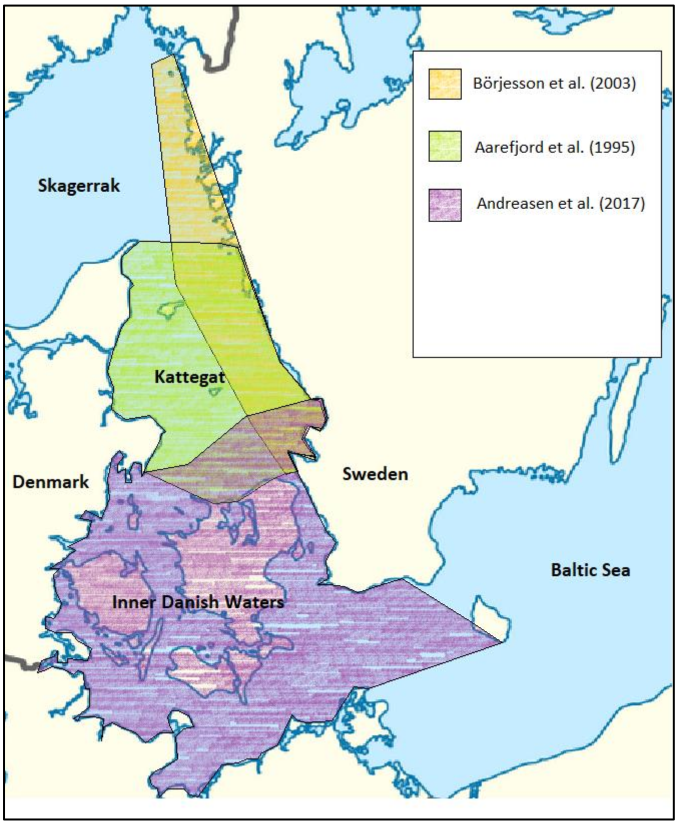

Figure 4: Approximate survey areas for the 3 stomach analysis studies included in the diet composition calculations.

3.3 Total cod consumption of harbour porpoise in the Kattegat

Using the mean, maximum and minimum daily consumption of harbour porpoises in the North Sea, Baltic Sea and the Kattegat presented in Table 3, as well as the abundance of harbour porpoises in the Kattegat calculated in Table 4 +/- one standard deviation, the annual consumption of fish could be approximated. Applying the mean, maximum and minimum diet composition values from Table 5 allowed for an estimation of harbour porpoise predation specifically on cod in the Kattegat (Table 6).

Table 6: Total annual fish outtake calculated from abundance and daily intake per porpoise, converted to tonnes per year.

	Average (tonnes/yr)	*Min (tonnes/yr)*	*Max (tonnes/yr)*
Total fish consumption	31 340	10 790	61 930
Total cod consumption	7 020	593	18 150

3.4 Size/age composition of cod in the diet

The size composition of several prey species, including Atlantic cod, was analysed by Andreasen et al. (2017) and Börjesson et al. (2003). Another study of the prey length composition in porpoise stomachs in the waters outside of Iceland was conducted by Vikingsson et al. (2003). The results of each respective study are presented in Table 7.

Table 7: Length distribution of consumed cod estimated from harbour porpoise stomach contents.

Study	Length	
	Mean (cm)	**Range (cm)**
Andreasen et al. (2017)	23.0	2.6–56.9
Vikingsson et al. (2003)	22.4	4.7–51.4
	Mean (cm)	**SD (cm)**
Börjesson et al. (2003)	28.1	+/- 5.8

3.5 Spatio-temporal diet factors

Andreasen et al. (2017) showed that harbour porpoises in the Western Baltic Sea, both juvenile and adult, eat a higher weight proportion of cod during the second half of the year compared to the first (Table 8). These seasonal changes can be compared with the seasonal migration of harbour porpoise presented by Sveegaard et al. (2011), where satellite tracking showed that the harbour porpoises in the Kattegat migrate seasonally in and out of the Kattegat (Figure 5).

*Table 8: Weight percentage of cod in harbour porpoise stomach content, by quarter of year (*Andreasen et al. *2017)*

Quarter	Cod proportion (W%)	
	Juvenile	**Adult**
1Q (January-March)	7.3	31.8
2Q (April-June)	18.4	18.6
3Q (July-September)	51.6	41.7
4Q (October-December)	30.0	55.4

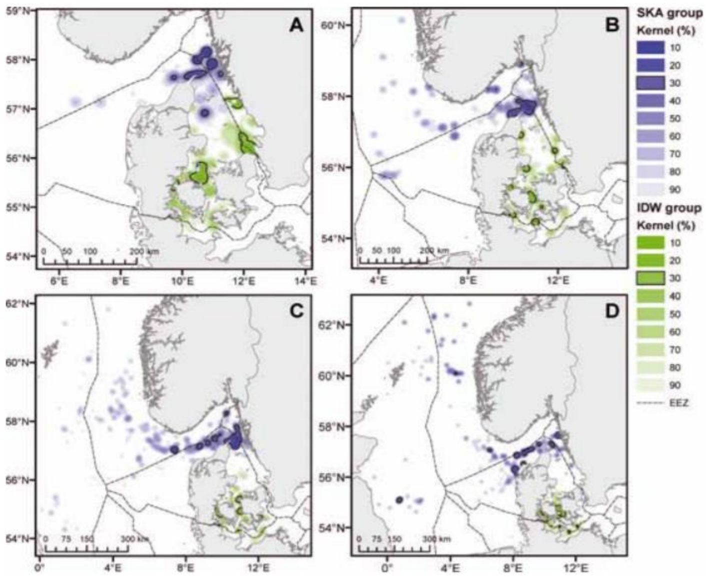

Figure 5: Sesonal distribution of harbour porpoise in the Kattegatt-Skagerrak area, from sattelite tracking of 64 harbour porpoises between 1997 and 2007. The green areas indicate the distribution of the population that lives in the southern part of the Kattegat (IDW=Inner Danish Water), the blue population is housed in the northern part (SKA=Skagerrak). Figure 5A indicates the distribution for the spring, B for summer, C for autumn and D for winter. Maps from Sveegaard et al. (2011).

Andreasen et al. (2017) also made a computerized GAM (Generalized Additive Model) analysis of how species occurrence varied over the surveyed time period of 1980–2011. The analysis showed that the occurrence of cod in harbour porpoise stomachs in the Western Baltic decreased markedly in the 1980s and then increased back again in the 1990s (Figure 6).

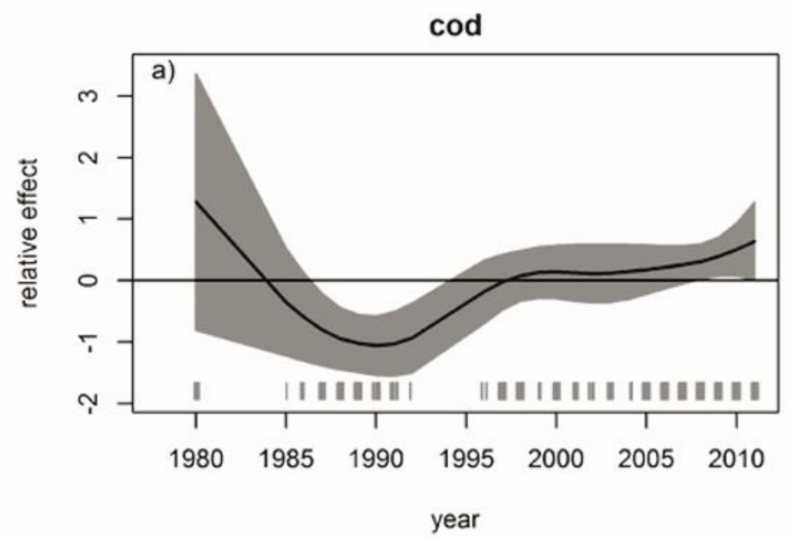

Figure 6: Graphical representation of a GAM (Generalized Additive Model) analysis of cod occurrence in harbour porpoise stomachs in the Western Baltic in the years 1980–2011 (Andreasen et al. 2017)

4. Discussion

Current information on the harbour porpoise populations in Kattegat is somewhat scarce. The largest abundance survey project has only been conducted 3 times, with 11 years between the surveys. The latest of these surveys provided an assessed abundance of 23 190 (15 550-30 830) harbour porpoises in the Kattegat area. Diet composition data for harbour porpoises in the Kattegat are generally obsolete, and the most recent analysis made uses samples almost exclusively from the Inner Danish Waters, with a very small fraction being from the actual Kattegat itself. Even in this recent study, the sampling period was 1980-2011, so the samples from Kattegat are still not guaranteed to be more recent than the other reviewed studies.

For this reason, an accurate data input of harbour porpoise predation cannot currently be applied to Kattegat cod stock assessment models. More concentrated data into the abundance and diet of harbour porpoise should be collected, with considerations towards spatio-temporal differences between the sample porpoises, and towards the size and age of the prey and the size, age and sex of the porpoise itself.

While this data is (hopefully) collected, a rough estimation of harbour porpoise predation on Kattegat cod can be provided by applying data on how diet composition of harbour porpoise varies seasonally to the current available data on harbour porpoise feeding habits. These rough approximations will not be sufficient to apply to stock assessment models in the long term, but can help in filling the void of knowledge that exists right now about harbour porpoise, and prevent potential population crises that may occur in the short term in the volatile populations of cod and harbour porpoise that are currently housed in the Kattegat.

4.1 Evaluation of current data

My evaluation of current data has shown that some of the data required to estimate harbour porpoise predation on the Kattegat cod stock exists. I also conclude that an approximate length distribution of cod in the diet of harbour porpoises - which can be translated into an approximative age distribution of prey - can be constructed.

To create a valid input into a cod stock assessment model, the data also need to be comparable to the timeline of the model itself. For this, the input values must cover the same time span as the model. In the cod stock assessment reports from ICES (2012, 2017), the input data are annual values and have been for several decades. As such, annual values for the data input from harbour porpoise studies are ideal, however as generation times of porpoise are quite a bit longer than that of cod, variations in abundance and diet will be slower, potentially allowing for data points that are more than a year apart. Available data is too out of date even from this perspective, however. The current abundance assessments have been many years apart which makes the data unreliable in comparison to the stock size assessments available for Kattegat cod, and making interannual variations in harbour porpoise population size hard to assess.

When taking the diet data available into consideration, the quality of current knowledge can be questioned. Most diet composition studies use a relatively low number of samples, spread over sometimes as much as 30 years. This causes problems where the samples used in the studies are subject to the sampling effect where random variations may give results not representative for the study as a whole, and the variations in prey composition and feeding habits during the sampling period are not taken into consideration. These factors make a reliable estimation of harbour porpoise diet compositions over time impossible to attain, as these temporal variations are very important to consider when applying the predation on stock assessment models for Kattegat cod.

As the data input in the model is also meant to be applied onto the entire porpoise population in the Kattegat, having diet composition data that can be assumed to be representative to the entire population is important. All studies found in this subject that had samples from the Kattegat were limited to morphological analysis of stomach content. This comes with additional issues where that method can only analyse what the individual porpoise has eaten within a few days of its death. As most studies are limited to stranded or bycaught animals, their recent feeding habits are most likely not representative of the feeding habits of the harbour porpoise population in the main Kattegat body of water. There is also a case to be made about the potential differences between datasets that can be caused by different sample material – For example, the study from Andreasen et al. (2017) used stomachs from stranded or bycaught animals, while Börjesson et al. (2003) analysed stomachs from bycaught animals only.

Additionally, as there is currently no assessment program for harbour porpoise diet in the Kattegat, the data available for diet compositions and consumption rates are not exactly applicable in the current situation due to available data being out of time.

Research regarding the daily consumption of harbour porpoise is limited. Most studies were both conducted on animals in captivity and based on a very small sample size and, in Sergeant (1969)’s case, exclusively stranded samples. The physiology of these animals were analysed, and while the results are representative for all harbour porpoises, the sample size is still very small which makes results less reliable statistically.

The results used in this study was from Andreasen et al. (2017), where an estimated mean daily consumption mass was calculated for harbour porpoise in the Western Baltic using the diet composition in the samples of that study, as well as three levels of estimated energy requirement based on former research into the energy requirements of the harbour porpoise – 10 MJ, 20 MJ and 30 MJ. The potential uncertainties of the diet composition portion of these calculations are explained above, including bias due to all samples being from stranded or bycaught animals, possible misjudgement of prey size due to the equations being more suited to the growth rate of cod in the North Sea, and a very large portion of the samples not being from the actual Kattegat itself. It is, however, still considered as a reliable source of information on harbour porpoise daily consumption. Further studies into this subject is needed.

Prey length composition data does not have to be geographically limited, as it is mostly tied to the physiology of the porpoise which is generally similar between populations. The three studies that were included for their length distribution data (Börjesson et al. 2003, Andreasen et al. 2017, Vikingsson et al. 2003) all found that the majority of cod that was eaten by harbour porpoise were less than 30 cm in length. Börjesson et al. (2003) found the highest mean prey length, 28.1 cm, but also stated that the length distribution found was in line with a normal distribution, leading the the conclusion that the majority of the prey cod found was below 30 cm in length. Vikingsson et al. (2003) also found the length distribution to have two peaks in occurrence – One at 5-13 cm and one at 25-35 cm in length. Applying length-to-age ratios of the Kattegat cod stock to these numbers could give additional information on what age classes are most vulnerable to harbour porpoise predation.

Overall, the data required to make a reliable assessment of harbour porpoise predation on the Kattegat cod stock is unavailable, obsolete or insufficient. A logical next step in this field of study is related to this relative lack of data. Additional studies in all mentioned fields within the coming years would naturally increase the reliability of data, and adding analyses of stable isotopes and fatty acids to diet analyses can provide additional long-term diet data compared to the morphological stomach content analyses that have been conducted so far (Mahfouz et al. 2017).

Pierce et al. (2007) analysed data sets on harbour porpoise diet and feeding habits and found that the most impactful source of variation in a diet composition study of harbour porpoises off the Scottish coast by Santos et al. (2003) was sampling errors, i.e. errors derived from only analysing a small number of stomachs compared to the overall population. In the same study, the variation in population-wide daily food consumption results from the same dataset was mainly derived from uncertainties in the energy requirements of the harbour porpoise, as well as uncertainties in population size estimates.

These analyses further support the assessment made in this study that more numerous and more recent samples would be highly valuable in making more accurate estimations of harbour porpoise predation. This process is currently not in progress, however, and assembling a sample of that size would take many years, which may be a problem when it comes to managing the populations of cod and harbour porpoise in the Kattegat. In Pierce et al. (2007) there is also mention of *stratification* of samples, which could be explained as identifying parts of a group of samples that differ in diet, identifying what variables cause these variations, and then weighting the results based on these differences. If a proper stratification cannot be found, results are likely to be biased towards years with a high rate of samples. One variable that could be used in making such a stratification could be seasonal variations in diet data. For example, seasonal and annual diet data like that presented in Andreasen et al. (2017) could be used to analyse how the proportion of cod in harbour porpoise diet varies with seasonal or annual differences in spatial distribution and prey availability. This information could then potentially be used to fill the gaps of knowledge in how diet composition differs from year to year, compared to annual differences in cod abundance.

4.2 Harbour porpoise predation calculations

The studies reviewed in this project provide an estimation of harbour porpoise predation of 7 020 (593-18 150) tonnes of cod per year. The large variation of this result comes from the large variations in diet composition found in the Kattegat as well as the variation in estimations of daily food consumption.

This information could potentially be used to make a prognosis of how the predation pressure will change with the assessed changes in Kattegat cod availability in the future. However, this would require additional and more recent diet composition data, and as such an assessment project currently does not exist, current samples are not being provided for diet analysis, and will not be provided either until such a project is funded and conducted. In the absence of such samples, applying data on seasonal and annual variations in diet composition could be key to making an assessment of how harbour porpoise predation will change with future changes in prey availability.

The seasonal diet composition of Andreasen et al. (2017) shows that the higher proportion of cod in stomach content can be found in the second half of the year. This can be compared to the mapping of seasonal migrations of harbour porpoises in the Kattegat done by Sveegaard et al. (2011). As the samples gathered in Andreasen et al. (2017) mostly come from the Belt Sea, Western Baltic and southern Kattegat, the data can be compared to the Inner Danish Waters population of Figure 6. When comparing the two data sets, the conclusion can be drawn that the largest proportion of cod is eaten in the second half of the year, when most of the population has moved south, out of the Kattegat. This should be taken into consideration when applying values like these to the Kattegat cod stock, as the annual values are likely disproportionately higher than the real values for cod eaten by harbour porpoise while in the Kattegat. Additionally, in the specific case of Andreasen et al. (2017), most of the samples are from outside of the Kattegat which makes it increasingly difficult to find a way to apply these newer data to the Kattegat population. It is noteworthy that the satellite tracking conducted in the survey by Sveegaard et al. (2011) only observed 64 porpoises (38 in the Inner Danish Water population and 26 in the Skagerrak population), and with such a small sample size there is always the risk that they are not representative of the entire populations. The samples from Andreasen et al. (2017) are also not entirely equally distributed quarterly, as for example the study discusses that the number of samples from Q1 are rather low and could be subject to the sampling effect.

The GAM analysis of Andreasen et al. (2017) (Figure 6) of cod content in harbour porpoise stomachs in the Western Baltic Sea over the years 1980-2011 shows a decrease during the

1980s and a subsequent increase during the 1990s. Comparing this data to the SSB of the Western Baltic cod stock, which shows a similar curve during the 1980s and 1990s (ICES 2012) could reveal vital information on how harbour porpoise prey choice varies with availability of key prey species.

4.3 Comparisons to research in other areas

Studies on harbour porpoise diet compositions have been made for several areas outside of the Kattegat, the most proximate of which are presented in Table 2. Almost all studies, from all areas, were conducted using stomach content analysis. As previously discussed, this method is lacking in providing diet data for more than a few days past. Major variations in choice of diet can be found between survey areas, however.

In a paper by Santos & Pierce (2003), comparisons between several studies from various places in the distribution area of the harbour porpoise are made. In a timeline of 1989-1996, results of widely varying preys of choice could be found. Stomach content analysis of 100 stranded or by-caught porpoises along the British coast presented gadoids (whiting, haddock, Norway pout *Trisopterus* esmarkii and pollack) as the most important prey (Martin 1996). In the same time period, porpoises from Scotland had a higher focus on sandeels, while in the Netherlans, gobies, dragonets and squid *Loligo forbesi* were significantly more important. A small sample from Galicia showed a highly diverse diet composition, including some species only present on the Galician coast (Santos 1998). In all the comparisons made, the only areas where cod made up a significant part of harbour porpoise diet were along the Danish coast and in the Baltic Sea. This supports the theory that cod is a key prey species for harbour porpoises near the Kattegat area.

These major differences in diet go to show that extrapolating the prey preference of harbour porpoises in one area to another cannot be readily done. The diet composition of harbour porpoises in a given area can quickly change due to prey migrations, prey distributions and even potentially the local bathymetry of the waters (Bjørge 2003). It may be possible to correlate the prey of choice found in these areas to the local distributions of prey in the area, and from these results create a model for how harbour porpoise diet compositions vary with prey availability. These models could then, in theory, be used to make assessments of harbour porpoise predations on specific prey species in the area, given that sufficient prey distribution and porpoise population size data for that area are available.

Feeding rate data from other areas than the Kattegat are, in theory, directly applicable to the harbour porpoises within the Kattegat. Table 3 showcases that the daily requirement of harbour porpoises from many studies are in agreement with the assumed requirements used for harbour porpoises in the Western Baltic proposed by Andreasen et al. (2017). The differences in weight requirements are slightly higher, however, which is related to different assumptions of energy density in prey, and different choices of feed in the case of captive animals. This shows that when extrapolating feeding rates from one geographical area to another, the energy requirement value in MJ/day is more relevant to carry over than the weight requirement value in kg/day. If a weight requirement is requested, it could be more accurate to use average energy density of the prey species available in the area, given the opportunistic feeding habits of the harbour porpoise.

It should also be noted that, as in the case of Yasui and Gaskin (1986) where stomach content data was analysed from the Bay of Fundy in Canada, energy requirements can be higher or lower depending on geographical location. While it is still within the assumed limits proposed in Andreasen et al. (2017), it should be considered that average energy requirements of a population may move towards the lower or higher end of those limits depending on the conditions of the area. Identifying what factors impact if the energy requirements will be higher or lower in a given area may be helpful in transferring energy consumption rate data for harbour porpoise between geographical locations. As energy requirement data are probably the hardest to attain in these analyses (Santos et al. 2014), being able to make relatively accurate assumptions that can circumvent the need for collecting these data would also help in making diet analyses much easier to do.

Material from studies outside of the Kattegat area could also potentially be used to gain information on the variations of diet compositions based on the harbour porpoises' age, sex and size. These variables could be easier to extrapolate from area to area, as they are tied to parts of the porpoise's physiology rather than ecological factors of the area itself. Factors such as cause of death are also available in some studies from other areas. Gaining information on additional variables such as these can improve the accuracy of a predation assessment.

4.4 Potential sources of error within source material

Within the methods of the stomach content analyses (presented in Börjesson et al. (2003), there were some pieces of information that were missing that could influence the results of this study. All porpoises less than 1 year old were excluded from the analysis of Börjesson et al. (2003), as these were considered uncharacteristic for the portion of the harbour porpoise population at which the diet analysis was directed. Meanwhile, there was no such distinction when assessing the abundance in the SCANS-III survey. Additional information on the proportion of porpoises not included in the stomach content analysis would necessary when making an estimation of the predation from the entire population of harbour porpoises. For example, the distribution of juveniles and male/female adults in the population would shed light on this proportion.

Additionally, sagittal otoliths were the primary indicator used to estimate number of prey, and there is a possibility that some may have been lost due to digestion, leading to an underestimation of prey number. In addition, while there were procedures in place to estimate the level of degradation of the analysed otoliths, there is still a risk that the sizes of the prey fish are underestimated due to a larger-than-expected degradation of the sagittal otolith (Especially in stranded samples where digestion may have been going on post mortem). This could result in an error where the actual number or size of prey is larger than the assessed result, a possibility that must be taken into consideration when making population viability analyses based on these numbers. An underestimation of number or size of prey could mean that recommended efforts based on these data end up being insufficient.

When making size regressions to determine average size and length of the cod whose remains were found within stomach content in Andreasen et al. (2017) and Börjesson et al. (2003), two separate size regression equations were used. Andreasen et al. (2017) used the regression presented in Leopold (2001), while Börjesson et al. (2003) used the one presented in Härkönen (1986). When making regressions focused on cod from the Kattegat, the regressions from Härkönen (1986) are more accurate to the reality. Leopold et al. (2001) presents a regression that is more like the growth rate of fish in the North Sea. As such, the size composition of Börjesson et al. (2003) is more reliable when focusing on samples found in the Kattegat.

One potential source of misleading data could come from the method used for calculating the weight percentage comprised of cod within the harbour porpoise stomachs. In the stomach analysis study of Aarefjord et al. (1995), the *total* calculated mass of cod individuals was divided by the *total* calculated mass of all prey species individuals to create the weight percentage result presented. This means that if there are a) porpoises that have eaten a large mass of fish but a small mass of cod and b) porpoises that have eaten a small mass of fish, but almost exclusively cod, the former group will have a much larger effect on the result compared to the latter group. This also applies to the inverse situation. The study from Börjesson et al. (2003) calculated the mean prey weight in each stomach, and then used the mean from all stomachs to apply to the mean weight of all fish eaten by porpoises in the study. The method for calculating mean weight percentage in the study from Andreasen et al. (2017) matched that of Börjesson et al (2003).

Another issue that may arise when calculating amount of Kattegat cod falling prey to harbour porpoises is the fact that the population of cod in the Kattegat is comprised not only of the local Kattegat cod stock, but also juvenile cod from the North Sea stock intermix (ICES 2017). Genetic analyses to determine the relative proportions between individuals from each of these stocks will help greatly in more accurately determining the proportion of the harbour porpoise predation that is being applied specifically to the Kattegat cod stock.

4.5 Conclusion

Many of the values presented in this study are presented as “estimates” or “approximations”, which is indicative of that the data available are not adequate to make any precise measurements, but rather to make prognoses on how the predation on harbour porpoise *may* come to affect the cod stock in the Kattegat. Diet composition data is also out of date and to a large extent from outside the bounds of the Kattegat. With additional data points and more thorough research, these prognoses can become more reliable.

The data that has been compiled within the confines of this study can be useful in furthering analysis into, and potentially even completing a rough approximation of how harbour porpoise predation possibly could affect the Kattegat cod stock. The calculations made in this study present an annual cod consumption from harbour porpoises in the Kattegat of approximately 7 020 tonnes (593-18 150 tonnes). Variations in this consumption estimate are due to variations in abundance assessment, diet composition and daily consumption rate data. Comparing this to an estimated annual less than 2000 tonnes consumed by harbour seals in the Kattegat during the last years (Karl Lundström, SLU, personal communication), and a total fishery landing of 299 tonnes in the Kattegat from Sweden, Denmark and Germany combined in 2015 and a discard of 401 tonnes for Sweden and Denmark in the same year (ICES 2017), suggests that harbour porpoise may contribute significantly to the natural mortality of the local cod stock. Although a very rough approximation, this information provides a possible range of the harbour porpoise predation pressure on cod in the Kattegat, which may be useful in assessment and management of factors contribution to the natural mortality of the Kattegat cod stock .

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